Does thermal plasticity affect susceptibility to capture in fish? Insights from a simulated trap and trawl fishery.

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Abstract

In fishes, physiological and behavioural traits can correlate with vulnerability to capture with fishing gears, highlighting the capacity of fisheries selection to drive phenotypic change in exploited populations. There remains a paucity of information regarding how different fishing gears may select on phenotypic traits and how relationships between individual traits and capture vulnerability change across environmental gradients. By simulating the capture process in a trawl and trap using wild minnows acclimated to different temperatures, we investigated how contrasting fishing gears select on behavioural and physiological traits, and how this selection is modulated by temperature. Despite similar risk of capture in each gear, selection differed between traps and trawls. Fish exhibiting low spontaneous activity were at greater capture risk in the trawl across all temperatures, while traps showed no selection except at 24°C. No relationships between physiological traits and capture vulnerability were found, except between swim performance and trap capture vulnerability at 24°C. This study demonstrates that fisheries selection on individual traits is likely context-specific, depending on both fishing gear type, and environment.

Keywords: Physiology, Behaviour, Fisheries Selection, Metabolism

INTRODUCTION

In fishes, physiological and behavioural traits often correlate with an individual's vulnerability to capture by fishing gears (Diaz Pauli *et al.* 2015; Killen *et al.* 2015a; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Redpath *et al.* 2010). These traits may therefore be under selection in exploited fish populations. Selective removal of fish exhibiting specific behavioural or physiological traits may drive shifts in the phenotypic composition of fish populations by eroding overall trait diversity (Arlinghaus *et al.* 2017; Diaz Pauli and Sih 2017), but may also influence evolutionary responses if traits under selection are heritable (Arnold 2010; Diaz Pauli and Sih 2017; Enberg *et al.* 2012; Heino *et al.* 2015; Hollins *et al.* 2018). Assessing the capacity of fisheries to drive phenotypic change in wild fish populations is of increasing conservation and management concern (Dunlop *et al.* 2009; Laugen *et al.* 2014; Ward *et al.* 2016), but requires comprehensive understanding of the mechanisms of capture employed by different fishing gears; how individual traits influence vulnerability to capture in these gears, and how these relationships are modulated by the environment (Diaz Pauli *et al.* 2015; Hollins *et al.* 2018; Horodysky *et al.* 2015).

Fishing gears can be categorised as either active or passive, based on their mechanism of capture. Active gears, (*e.g.* trawls) pursue or encircle target fish, while passive gears (*e.g.* traps) rely on fish to approach and interact with the fishing gear to be captured. These contrasting mechanisms of capture mean that traits which correlate positively with susceptibility to capture in one gear may show the opposite or no relationship with capture vulnerability in another (Diaz Pauli *et al.* 2015). For active gears, physiological traits linked to individual swim performance may be particularly relevant in terms of determining capture vulnerability (Killen *et al.* 2015b; Kim and Wardle 2003; Marras *et al.* 2010). Trawl

67 nets employed by fishers are towed at a speed chosen to progressively exhaust pursued fish, causing
68 fish in the path of a trawl to engage in burst-and-coast swimming to maintain station ahead of pursuing
69 nets, before eventually succumbing to fatigue and being caught (Rose 1995; Ryer *et al.* 2009;
70 Underwood *et al.* 2015; Winger 2010; Yanase *et al.* 2009). Pursued fish have also been observed
71 entering trawls head-first (Rose 1995; Underwood *et al.* 2015), which has the potential to disrupt
72 selection on swim performance (Hollins *et al.* 2019), although the mechanisms underlying this behaviour
73 are unclear. Individual burst-swimming performance is linked with anaerobic metabolic capacity (Killen
74 *et al.* 2015a; McKenzie 2011; Svendsen *et al.* 2015), and it has been shown that fish exhibiting high
75 anaerobic metabolic capacity may be less vulnerable to capture by trawls while swimming in groups
76 (Hollins *et al.* 2019; Killen *et al.* 2015a). Traits related to aerobic metabolism also have the capacity to
77 influence individual fish's vulnerability to capture in active gears. Aerobic scope (AS) is the difference
78 between an animal's minimum and maximum rate of aerobic metabolism (standard metabolic rate, SMR
79 and maximum metabolic rate, MMR, respectively), and so represents the capacity of an organism to
80 simultaneously deliver oxygen to physiological processes beyond those required for maintenance. While
81 previous experiments have not found relationships between AS and vulnerability to trawl capture
82 (Hollins *et al.* 2019; Killen *et al.* 2015a), relationships between physiological traits and capture
83 vulnerability may only arise under specific contexts. For example, where fish are pursued by a trawl in
84 temperatures beyond the thermal optima for AS, high AS individuals may be at an advantage, as they
85 may have sufficient AS remaining to fuel aerobic swimming, or recovery from exhaustive exercise.

86 Physiological traits may also underpin a range of behaviours which can influence individual fish's
87 susceptibility to capture in passive fishing gears (Andersen *et al.* 2016; Arlinghaus *et al.* 2017; Diaz Pauli
88 and Sih 2017; Metcalfe *et al.* 2016). SMR is a physiological trait which shows wide intraspecific variation
89 (Burton *et al.* 2011; Metcalfe *et al.* 2016) and is intrinsically linked with individual fish's energetic
90 demands and, in some contexts, behavioural traits related to boldness and foraging activity (Killen *et al.*

2011; Killen *et al.* 2012a). Individual fish with high SMRs may therefore be more likely to engage in foraging behaviour at any given time, and so be more likely to encounter fishing gears (Hollins *et al.* 2018), or to inspect bait in a passive gear once it has been encountered (Biro and Post 2008; Hessenauer *et al.* 2015; Hollins *et al.* 2018; Klefoth *et al.* 2017; Svendsen *et al.* 2015). Fish that display these active, risk-prone behaviours may also possess increased AS to accommodate the energetic demand of a more active lifestyle (Killen *et al.* 2012b; Killen *et al.* 2014; Redpath *et al.* 2010). Therefore, AS may also influence individual vulnerability to capture in passive gears.

While behavioural and physiological traits can correlate with capture vulnerability in both laboratory and field studies (Biro and Post 2008; Diaz Pauli *et al.* 2015; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Redpath *et al.* 2010; Wilson *et al.* 2011), these relationships can be inconsistent (Louison *et al.* 2018a; Vainikka *et al.* 2016). For example, Klefoth *et al.* (2017) found that bold carp (*Cyprinus carpio*) were selectively removed by angling, while Wilson *et al.* (2011) reported the opposite trend in bluegill sunfish (*Lepomis macrochirus*), and no relationship between the two was found in perch (*Perca fluviatalis*) by Vainikka *et al*. (2016). This could in part be due to the influence of environmental factors on relationships among traits (Killen *et al.* 2013). Many traits which may influence individual fish's susceptibility to capture are labile, and environmental conditions can act to constrain the expression of these traits among fish populations (Domenici *et al.* 2013; Johansen *et al.* 2014; Meuthen *et al.* 2019; Stoner 2004), or otherwise alter relationships between expressed traits (Killen *et al.* 2013). More empirical work is needed to improve our understanding of how environmental factors alter correlations among labile traits, and to inform us on which traits are available as targets for direct or correlated selection in the context of fisheries.

Environmental temperature is especially likely to alter relationships among metabolic and behavioural traits which in turn may affect susceptibility to capture in fish. Metabolic rates of ectothermic animals increase with temperature, in turn increasing baseline energetic demand.

Increased demand for resources may subsequently alter individual behaviour, if fish must spend more time foraging or be more aggressive to secure sufficient resources. If any increase in SMR due to warming is not met with commensurate increases in MMR, then AS will be reduced, reducing the capacity to perform simultaneous aerobic physiological processes. This constrained aerobic capacity may limit the phenotypic expression of fish, reducing phenotypic diversity of fish populations, and therefore the capacity of fishing gears to select on specific traits. Elevated environmental temperature can also influence individual traits independently of effects on AS, particularly those related to swim performance (Hvas *et al.* 2017). Elevated temperatures increase the maximum contraction velocity and power output of red muscle fibres (Rome 1990; Rome *et al.* 1992), postponing the recruitment of anaerobic white muscle when swimming at high speeds, delaying the onset of fish fatigue, for example. Finally, it is unlikely that reaction norms for a trait determining vulnerability to capture across temperatures will be identical for all fish within a population (Cavieres and Sabat 2008; Maldonado *et al.* 2012). Accordingly, as temperature changes, so may the individuals which exhibit the greatest vulnerability to capture.

Experimental lab-based approaches to studying fisheries selection permit precise control over the myriad factors which may influence fish capture vulnerability, allowing us to isolate the contribution of specific factors of interest (Thambithurai *et al.* 2018). Similarly, small scale recreations of fisheries permit control over the capture process itself, allowing us to facilitate encounters between fish and fishing gears, and focus on how selection operates at specific stages of the capture process (Hollins *et al.* 2018). Surrogate species have been used in a number of experimental approaches to studying fisheries selection (Conover and Baumann 2009; Reznick and Ghalambor 2005), and provide several advantages when compared studying wild, commercial species already exposed to fisheries selection for decades. In this study, we used European Minnow (*Phoxinus phoxinus*) to investigate the effects of thermal plasticity on the capacity for trap and trawl fisheries to select on behavioural and physiological traits. Using this

approach, we aimed to address the following questions: i) Does acclimation temperature affect vulnerability to capture in active and passive fishing gears? ii) Does acclimation temperature affect which traits are related to capture vulnerability in active and passive gears? The results here will further our understanding of how environmental factors modulate trait-based selectivity by fishing, a topic that to date has been largely overlooked**.**

METHODS

All minnows were initially held at 16°C, at which point baseline measurements of physiological and behavioural traits were taken (Figure 1). Fish were then haphazardly assigned to one of two groups, dividing the population in half. Half of the fish were subsequently kept at a constant 16°C throughout the remainder of the study, to act as a temporal control, while the remaining half were sequentially acclimated to 20 and 24°C. European minnow occupy freshwater environments at temperatures of 2-20°C .Both the control and first acclimation temperatures therefore represent conditions likely experienced by wild fish, while 24°C was anticipated to constrain the aerobic metabolic capacity of experimental fish, and roughly corresponds to projections of maximum temperature increases in freshwater systems in the UK by 2100 (Robins *et al.* 2016), in accordance with IPCC high emissions scenario projections . After each acclimation period, both the warm acclimated and control fish had all physiological and behavioural measurements repeated, in addition to being subjected to both a simulated trawl and trap fishery (Figure 1).

Experimental Animals

All minnows *P. phoxinus* used in this study were sourced from the wild during October 2016, collected via a large dip-net from the River Kelvin. Fish were then kept in aerated tanks (100x40x40cm) supplied with recirculating UV treated water maintained at 14-16°C for 6 months before experimental procedures began. A total of 72 similar sized minnows (7.45± 0.56cm and 4.84± 0.64g, mean

length/mass ± SD) were subsequently split across 6 aerated tanks (50 x 40 x 40cm) so that each tank housed 12 individuals.. Each tank received identical water, contained a shelter, gravel substrate and plastic plants, and all fish were kept on a 12L: 12D light cycle. During this time, minnows were kept on an *ad libitum* feeding regime, and were fed a mixture of commercial feed and bloodworm. Once fish were assigned to their respective tanks, they were anaesthetised using benzocaine, and implanted with individually coded PIT tags, to allow identification. Fish were then allowed 1 week to recover before experimental procedures began.

Temperature Acclimation and Measurement of Individual Traits

At each acclimation temperature, measurements of behaviour, swim performance, and physiological traits were taken. In all cases fish were fasted for 48 h before each procedure. The order of testing the tanks was haphazard but conformed to a general pattern of alternating between tanks assigned to the 'control' and 'warm acclimation' treatments on successive days. Fish were assayed for swim performance first, with half the fish from each of two tanks trialled per day. Once these procedures had all been completed at 16°C for all fish, temperature acclimation began. Tanks 1-3 were maintained at 16°C for the duration of the experiment (Figure 1), and so tank conditions remained exactly as described above. Tanks 4-6 were incrementally warmed to 20 °C over a period of a week, and then left to acclimate at a constant 20°C for 4 weeks before traits were re-measured, alongside trap and trawl vulnerability (Figure 1). Tanks were selected for testing in the same way as the previous round of measurements, although all respirometry, activity assays and fishing vulnerability assays were now conducted at the tank's respective acclimation temperature. After a recovery period of at least 3 days, all fish were then profiled for vulnerability to capture in whichever gear they had not yet faced. Once all assays were complete, fish were maintained at their acclimated temperatures for twomonths (16°C and 20°C), before a final temperature increase could begin (Figure 1). Again, tanks 1-3 remained at 16°C, while tanks 4-6 were incrementally warmed from 20°C to 24°C over a week, before being left to

acclimate at their warmer temperature for a month. After this time, fish were assayed again, following an identical schedule to that described for sampling at T2 (figure 1).

Swim Performance

Individual swim performance was determined for each fish using a constant acceleration test (CAT, Killen *et al.* 2015). CATs were performed after each acclimation temperature had been reached over the course or 14 days at each of T1, T2 and T3. For each CAT fish were placed into the working section (45x14x14cm) of a 30-l Steffensen type swim tunnel (Loligo systems, Tjele, Denmark), designed to exercise fish at controlled speeds in non-turbulent water with a uniform velocity profile. All CATs were performed at the individual fish's acclimation temperature. Once within the swim tunnel, the lid was tightly bolted on, and the fish left to acclimate for 30 minutes at a water velocity of 5cm s^{-1}, approximately 1 BL s^{-1}. Once acclimation was complete, water velocity was then increased by 2.5cm s^{-1} every minute. Water velocity continued to be increased until the fish fell against the retaining grid at the back of the working section of the swim tunnel and did not resume swimming for 5 s. The speed at which this occurred was taken as each individual's maximum swim speed (U_{max}) and represents the fish's maximal swim performance, fuelled through both aerobic and anaerobic metabolism.

Behaviour

Once all fish had been assessed for swim performance, fish were then assessed for behavioural traits at each of T1, T2 and T3. All fish were left to recover in their tanks after swim trials for at least 10 days before behavioural trials began. Individual fish activity was determined using an open field assay using an 80x20cm behavioural arena divided into 2 sections separated by a removable plastic divider. All activity assays were conducted within a metal scaffold covered with opaque curtains which minimised potential disturbance to the fish. Each divider was attached to a simple pully system using fishing line which allowed it to be lifted and lowered from outside of the frame, without disturbing fish. Four arenas

were placed side-by-side within the frame so four fish could be profiled simultaneously. Fish activity throughout these trials was recorded using two cameras (Logitech, C920 HD Pro Webcam) fixed to the top of the frame so that each camera had two tanks in frame. The first section of the behavioural arena consisted of a small acclimation area (10x20cm), with gravel substrate, where fish were placed at the beginning of the trial. Here, fish were allowed to acclimate for 10 minutes, before the first plastic divider was withdrawn, and the second section of the arena became visible to fish. This second 70x20cm section consisted of an open field, with no substrate or shelter present. Fish were then allowed to swim freely about the arena for 20 minutes. Activity of fish was subsequently quantified from recorded videos and determined as the amount of time fish spent active in the open field section of the arena during the middle 10 minute portion of the activity trial. A fish was defined as 'active' once it had moved 1 body length away from its starting stationary position and was 'inactive' once the fish remained stationary (*i.e.* resting on the tank bottom with no tail movement) for 5 seconds. The middle 10-minute section of the video was used to quantify activity to minimise the potential impact of removing/replacing the arena dividers on fish behaviour, and the 5-minutes either side of this period were not used.

Respirometry

Immediately after behavioural assays for a tank of fish were complete, all fish were subjected to intermittent flow respirometry to provide estimates of metabolic phenotype (SMR, MMR, and AS) one tank at a time. Estimates of maximum metabolic rate (MMR) were achieved by manually chasing individual fish to exhaustion for a period of 2 minutes in a circular plastic tank (50 cm diameter) with a water depth of 10 cm. By the end of the chase period, all fish ceased attempting to escape from being chased and were determined exhausted, and so were exhibiting maximal rates of oxygen uptake as fish recover from prolonged anaerobic exercise (Killen, Norin and Halsey, 2017). Once exhausted, fish were quickly transferred to individual cylindrical glass respirometry chambers (75 mL volume) attached to an intermittent flow respirometry system (Killen, Nati and Suski, 2015; Thambithurai *et al.* 2018). Oxygen

content of the water within the closed respirometry circuit was quantified once every 2 s using a Firesting 4-channel oxygen meter and associated sensors (PyroScience GmbH, Aschen, Germany). The circuit itself comprised of the glass cylinder, and a length of gas impermeable tubing, through which water was constantly recirculated using a peristaltic pump. Respirometry chambers were kept within an aerated, rectangular, temperature-regulated water bath (at the tank acclimation temperature ± 0.1°C; 50 l) and were shielded from disturbance and direct light via an opaque plastic blind. Every 8 min, an automated flush pump would switch on for 3 minutes to flush chambers with fresh oxygenated water, and then switched off, sealing the respirometers to allow decreases in oxygen content to be determined and used in the estimate of rates of oxygen consumption.

Estimates of MMR were obtained by calculating rates of oxygen uptake for each 3-minute time interval throughout the first 30 mins of recovery immediately following exhaustive exercise. MMR (mg O_2 h^{-1}) was taken as the highest rate of aerobic metabolism during this period. After measurement of MMR, fish remained in their respective respirometry chambers overnight to allow estimation of SMR. Individuals were removed from their chambers the following morning at around 09:00, having remained in the respirometers for approximately 17 hours total. Once retrieved from the respirometry chambers, fish were measured for wet mass and standard length, so that effects of fish size on metabolic traits could accurately be accounted for. Background bacterial respiration was accounted for by measuring rates of oxygen depletion in each respirometry chamber 3 times each before fish entered the chamber, and after they were removed. The relationship between these start and end points were then used to interpolate estimates of background respiration during each closed cycle for the duration of the time fish were held in the chambers and subtracted from estimates of fish oxygen consumption. Whole animal SMR (mg O_2 h^{-1}) was estimated as the lowest 20th percentile of measurements taken throughout the measurement period (Chabot *et al.* 2016). Absolute aerobic scope (AS) was calculated as the difference between MMR and SMR.

Fishery simulations

All fish were individually subjected to a simulated trawl and trap fishery. All simulations were designed to replicate the capture process, after fish had already encountered fishing gears (Hollins *et al.* 2018), and were all conducted at fish's respective acclimation temperatures. Two tanks of fish were subjected to the fisheries simulations per day, with half of each tank exposed to the trawl, and the other half to the trap, so that half of each tank encountered a different gear type first. Fishery simulations were conducted at T2 and T3, over a period of 5 days in each instance, at least 2 weeks after the cessation of respirometry.

Trap

Trapping simulations were performed in a rectangular 120x60x60 cm arena filled to a depth of 14 cm, housed within a frame covered with opaque curtains to minimise disturbance to the fish. Fish behaviour throughout the trial was recorded using a Logitech, C920 HD Pro Webcam mounted in the centre of the top of the frame and attached to a laptop computer. This allowed us to unobtrusively monitor fish movements in real time. In this study, we used a replica trap measuring 12x12x17 cm made from a metal frame and green mesh to simulate the final moments of capture in a trap fishery: when a fish has encountered a gear and is deciding whether to approach and subsequently enter the trap. The trap had one inverted conical entrance of a diameter of 2 cm at one end, while a bait canister was at the other. The bait canister consisted of a 10 cm^3 plastic cylinder with several openings covered with a fine mesh, to allow the scent of the bait to diffuse into the behavioural arena, without spreading the bait itself. This canister was attached to a bloodworm-filled syringe kept outside of the frame of the behavioural arena via a length of rubber tubing. At the beginning of the trial, the fish was held in a clear plastic shelter with an opaque top at the end of the tank furthest from the trap. Here, the fish was given an acclimation period of 10 min before the trial began. Just before the acclimation period was over, the plunger on the

bait syringe was pushed, releasing an odour cloud for the trap to act as an attractant. The shelter was then lifted from around the fish, and the fish allowed to explore the arena and interact with the trap. The fish was given a maximum of 30 minutes to enter the trap, at which point the trial was stopped and the fish recorded as 'caught', and the time until capture noted, while if the fish did not enter the trap it was recorded as an 'escape'. Once the trial was complete, the fish were returned to their holding tanks and fed, and the water in the arena completely drained and replaced.

Trawl

Trawling simulations were conducted in a 90 l Steffensen-type swim tunnel (Loligo systems, Tjele, Denmark), designed to exercise fish at controlled speeds in laminar flow with a uniform velocity profile, thermoregulated at each tested fish's acclimation temperature ± 0.1°. The working section of the tunnel was 70 long x 20 x 20 wide cm, and with a 3cm thick foam false bottom fitted along its length. A modified lid for the working section was constructed, with a slit cut 30 cm from the front of the lid. This allowed a perforated plastic divider to be placed into the working section of the tunnel, dividing the working section into a 30cm front portion and a 40 cm rear portion. This allowed for the net to remain hidden from test fish during their acclimation period (see below). Prior to the first trawl trial, the swim tunnel was calibrated using a vane wheel flow meter (Flowtherm NT, Höntzch, Waiblingen, Germany), with both the divider present and absent. Trawl trials began with single fish introduced to the front half of the working section, ahead of the trawl net, and then allowed to acclimate for 30 minutes at a speed approximating 0.5 body lengths per second (BLs^{-1}). Following this acclimation period, water velocity was gradually increased to 58.25cm s^{-1} over a period of ~30s, while the divider was slowly pulled up, exposing the fish to the trawl net in the latter portion of the working section of the tunnel. In this study, a custom-made scale replica trawl net (Marine Institute, Memorial University of Newfoundland) was used to simulate the final stages of capture in a commercial trawl: the pursuit of fish as they attempt to maintain station ahead of the trawl mouth, and resist falling back into the net. A solid metal frame was

used to hold the mouth of the trawl open, and ensure its shape held during and between trials, while ensuring that the sides of the net were flush with the working section of the flume, and the centre of the top of the net flush with the underside of the lid. Two possible escape routes were left in the top right and left corners of the working section of the tunnel, each encompassing an area of 3x3cm. The trawl included escape routes to allow fish to avoid spending time in the net by passing past it, as well as swimming ahead of it. The bottom of the net included black rubber washers to imitate the rollers present on the footrope of a trawl and was weighted to prevent it lifting during a trial and presenting an alternative escape route. The top of the net included several orange beads spaced approximately 2cm apart along its length to replicate the appearance of buoys along the headrope in a commercial trawl and to provide a potential visual queue for orienting near the front of the net. Once the divider was up, and the trial speed attained, fish were left to swim at 58.25 cm s^{-1} in front of the trawl for a maximum of 10 minutes. If fish fell back into the trawl against the net mesh and did not resume swimming for 5 s, the trial was stopped and the fish recorded as 'caught', alongside the time until capture, whereas if it dropped back past the net through one of the potential escape route, the trial was stopped and the fish recorded as 'escaped'.

Statistical Analyses

All statistical analyses were performed in R.3.5.1 (R Development Core Team) using the survival (Therneau and Lumley, 2009), lme4 (Bates *et al.* 2016), MuMIn (Barton, 2015) and rptR (Stoffel *et al.* 2017) packages. To investigate how temperature affects overall capture vulnerability in each gear (question (i)), survival curves were compared for trawls and traps across acclimation temperatures for each round of fishing simulations individually. Comparisons of survival curves for each gear across temperatures were made using Cox proportional hazard models (Cox PH) using both time until capture (continuous variable) and whether or not the fish was caught (binary variable) as response variables, and acclimation temperature as the single predictor variable. The role of individual traits in determining

vulnerability to capture (question (ii)), was also assessed using Cox PH models fitted to each fishery simulation individually. All behavioural data used for Cox PH models were first log(n+1) transformed, while maximum swim speed was log transformed. Metabolic traits (SMR, AS, and MMR) used in Cox PH models were adjusted for mass by calculating the residuals from the linear regression of each metabolic trait against log transformed mass, and adding calculated residuals to the predicted value of that metabolic trait at the mean mass of all fish. The inverse log of these values was then taken, and used to account for confounding effects of body mass and growth on metabolic rates between successive measurements (McLean et al. 2018). Cox PH models addressing question (ii), used log(n+1) transformed behavioural traits, and adjusted metabolic traits as predictor variables, alongside log-transformed absolute max swim speed (cm s-1). Models of best fit were determined using maximum likelihood estimation, with non-significant interactions dropped sequentially, starting with those with the smallest β values, but were retained if their removal resulted in higher AIC values (ΔAIC >2 (Arnold 2010)), with assumptions of proportional hazards assessed using the cox.zph function within the survival package in R. Cox PH models can be used to determine temperature mediated change in both overall capture vulnerability and patterns of selection in the simulated fisheries conducted here, however cannot describe the degree to which these patterns are driven by changes in the trait composition of the experimental fish populations. As a mechanistic approach linking individual traits to capture vulnerability in fish is an important aspect of understanding how patterns observed in experimental conditions may manifest under real fisheries scenarios, Linear Mixed Effects Models (LMEs) were used to investigate responses of individual fish traits to increasing acclimation temperature. LMEs investigating the role of temperature on the distributions of individual fish traits used 'Treatment' (a categorical variable with two levels: control and warmed) and 'Time' (a categorical variable with 3 levels, 'T1', 'T2' and 'T3') as fixed effects, and Fish ID as a random effect, predicting each individually measured fish trait. Each trait used had been transformed as described above, with the exception of swim speed,

which was instead normalised to body lengths s^{-1} (BLs^{-1}) to account for fish growth between trials. Assumptions of homoscedasticity and normality of residuals were examined by visual inspection of residual plots. Significance testing, alongside model r2 values were used to indicate the strength of observed patterns. R2 values included marginal (rm2) and conditional (rc2) r2 values which indicate the variance explained by fixed factors, and by both fixed and random factors, respectively (Nakagawa and Schielzeth, 2013).

Finally, the adjusted repeatability of each individually measured behavioural and physiological trait was also investigated using log(n+1) transformed behavioural traits, adjusted metabolic traits, and swim performance ($BL\ s^{-1}$) as response variables. Adjusted repeatability of each trait was calculated as described by Stoffel, Nakagawa and Schielzeth (2017) using variances calculated with LMEs and including fish ID as a random effect. Agreement repeatability of capture vulnerability was also calculated using binary caught/uncaught data, using fish ID as a random effect. The repeatability of both individual traits and capture vulnerability provides further context on the consistency and strength of patterns of fisheries selection on individual traits, and whether it is the same individual fish being caught by fishing gears under different scenarios.

RESULTS

Does acclimation temperature affect vulnerability to capture in active and passive fishing gears?

Risk of capture only increased in response to temperature for the trawl, not for the trap, and this effect of temperature on trawling vulnerability was only apparent at 24°C (figure 2, table 1). Probability of capture did not differ between fish trialled at 16°C and 20°C in the trawl ($p = 0.83$), or trap ($p=0.2$, table 1). Trawls conducted at T2 at 16°C caught 50% of fish (median chase time = 149s), and similarly trawls at 20°C caught 46.9% of fish (median chase time = 120s, Figure 2). In contrast, fish probability of capture in the trawl was higher at 24°C than at 16°C ($p=0.012$, table 1)), where 66.6% of fish were caught (median

chase time = 38s, Figure 2), compared to 37.5% of fish caught at 16°C (median chase time = 159s). Risk of capture in the trap was similar between both 16 vs 20°C (p=0.2), and 16 vs 24°C (HR=0.41, p=0.18) (table 1). Trapping at 16 and 20 °C caught 77.1% and 93.8% of fish (median capture times = 61 and 71s, respectivelywhile trapping trials conducted at T3 caught 81.2% of fish at 16°C (median capture time = 26s), and 80% of fish at 24°C (median capture time = 280s).

Does acclimation temperature affect which traits are related to capture vulnerability in active and passive gears?

Fish which spent more time moving in the open field assay (*i.e. w*ere more active) were less likely to be caught in the trawl at all temperatures, (p=0.04, p=0.025, for both trawl trials conducted at 16°C, and p=0.005, p=0.03 for trials conducted at 20°C and 24°C, Figure 3, Table 2), but there were no relationships between trawl vulnerability and any other trait. This selectivity regime was maintained across temperatures despite significantly higher fish activities found at 20°C (Supplementary Table S1, Supplementary Figure S1).Activity increased with temperature up until 20°C, before decreasing at 24°C. Although activity was consistently associated with capture vulnerability in the trawl, and was found to be a repeatable trait, (Table 3) trawl capture vulnerability itself was not repeatable across or within temperatures (Table 4).This indicates that while selection on activity was consistent, capture vulnerability was not. No relationship between any individual trait and capture vulnerability was found in the trap at any acclimation temperature, except at 24°C, where fish with higher swim performance were at significantly lower risk of capture in the trap (p=0.008, Figure 4, Table 2). This relationship between swimming performance and trap capture vulnerability was accompanied by a significant decrease in the swimming performance of fish at 24°C, while no differences in swim performance were recorded between 16°C and 20°C (Supplementary Table S1, Supplementary Figure S2). Vulnerability to trap capture was not found to be repeatable across temperatures (Table 4). Significantly higher SMRs,

398 which drove decreases in AS with temperature, were observed in fish acclimated to 24°C, although SMR,
399 AS and MMR did not correlate with capture vulnerability in either gear at any temperature (Table 2).

400 **DISCUSSION**

401 These results suggest that, during the critical phase of capture when fish are interacting with a deployed
402 gear, acclimation temperature has only a modest effect on risk for fish to be captured by either trapping
403 or trawling (Figure 2). Specifically, there was an increase in the proportion of fish captured by trawling
404 but at only the warmest temperature tested and there was no noticeable effect of temperature on
405 vulnerability to capture by trap. We also found differences in the traits associated with risk of capture
406 between active and passive gears, supporting the notion that different fishing gears can select on
407 contrasting phenotypes (Arlinghaus *et al.* 2017; Diaz Pauli *et al.* 2015; Uusi-Heikkilä *et al.* 2008, Figures 3
408 and 4). While metabolic traits were not correlated with vulnerability to capture by either gear at any
409 temperature, fish that were more active were less likely to be captured by trawl across all temperatures
410 (Figure 3), and fish with a higher swimming capacity were less likely to be caught by trap at the warmest
411 temperature (Figure 4). The relationship between swimming capacity and trap capture vulnerability at
412 24°C coincided with an overall reduction in swim performance and adjusted aerobic scope in 24°C
413 acclimated fish (Supplementary Figure S3), suggesting that at this temperature, fish were beyond their
414 thermal optimum. Establishing the capacity for fishing gears to select on physiological and behavioural
415 traits in fish populations, and how this is modulated by the environment could have important
416 implications for sustainable fisheries management (Horodysky *et al.* 2015; Laugen *et al.* 2014; Ward *et*
417 *al.* 2016). The results here highlight the capacity for environmental variability to interact with fisheries-
418 selection to yield phenotypic change in exploited fish populations.

419

In contrast to previous experiments investigating links between individual traits and capture vulnerability (Diaz Pauli *et al.* 2015; Hollins *et al.* 2019; Killen *et al.* 2015a), capture vulnerability across temperatures was not found to be a repeatable trait in its own right in either the trap or trawl (Table 4). Repeatability would likely have been reduced in the current study because we were measuring repeatability across temperature contexts (Stoffel *et al.* 2017). However, repeatability was also low for repeated measurements of fish from the control treatment conducted at 16^{o}C only. Previous experiments have tested trawl capture vulnerability in several fish simultaneously (Hollins *et al.* 2019; Killen *et al.* 2015a), which may have dampened any stochastic effects on capture probability, increasing repeatability of capture vulnerability. While low or absent repeatability of capture vulnerability in both gears may weaken the capacity for fisheries to select on individual traits, individual activity was consistently associated with trawl vulnerability across all temperatures. As such, while low activity fish were consistently at greater risk of capture in the trawl, the same fish are not caught each time. As temperature differences between trawl and trap vulnerability trials was likely a major cause of reduced repeatability in this study, this suggests that depending on acclimation temperature, different individuals are most likely to be captured by either trawl or trap. Repeated capture vulnerability trials within each acclimation temperature would be required in future work investigating the degree to which capture vulnerability is repeatable within as opposed to across thermal regimes.

We found no relationship between any of SMR, MMR, or AS and risk of capture by either gear at any acclimation temperature (Table 2). Metabolic phenotype has received considerable attention as a potential trait influencing susceptibility to capture in fish, particularly in passive gears (Hessenauer *et al.* 2015; Hollins *et al.* 2018; Louison *et al.* 2018b; Redpath *et al.* 2010; Thambithurai *et al.* 2018). Interestingly, swimming performance also showed no relationship with capture vulnerability in the trawl, in contrast with the findings of Hollins *et al.* (2019) and Killen *et al.* (2015). In the current study,

444 however, selection on anaerobic metabolic traits in the trawl would be most likely an indirect effect of
445 selection on swimming performance. As no relationship between swimming performance and trawl
446 capture vulnerability was found in this study, there was likely limited scope for the trawl to select on
447 correlated anaerobic metabolic traits. The disparity between these results may be attributable to the
448 design of the trawling simulations in each case. Both Hollins *et al.* (2019) and Killen *et al.* (2015) tested
449 fish trawl vulnerability in groups, while this study tested fish individually. This may have partially
450 decoupled trawl vulnerability from swimming performance, as it was found in the Hollins *et al.* (2019)
451 study that the relationship between anaerobic metabolic and capture vulnerability in the trawl was only
452 present when fish were tested alongside familiar conspecifics. Putatively, this pattern was driven by a
453 mechanism of familiar shoal mates providing stronger impetus for fish to engage in strenuous, anaerobic
454 swimming, than that provided by unfamiliar shoals, strengthening selection on swimming performance.
455 The inclusion of escape routes around the trawl in this study, which were not included in the Killen *et al.*
456 (2015) experiment, also had the potential to disrupt selection on swimming performance, by providing
457 opportunity for escape unrelated to the ability to solely maintain position ahead of the trawl net.

458 In this study, fish with a lower level of spontaneous activity had a higher risk of capture by trawl
459 (Table 2; Figure 3), agreeing with the findings of Diaz Pauli *et al.* (2015). This relationship between
460 individual activity and vulnerability to capture may be driven by more active individuals making use of
461 more space in front of the trawl, therefore being more likely to locate escape routes. Although some fish
462 were able to maintain sufficient swim speed to remain ahead of the trawl for the entire trial duration,
463 most uncaught fish avoided capture by utilising escape routes, therefore dampening the potential for
464 swimming ability to be a target for selectivity in this experiment. Interestingly, despite this reduced
465 capacity for swimming performance to influence capture vulnerability, risk of trawl capture was higher
466 at 24°C (Table 1, Figure 2), coinciding with a reduction in swim performance seen in 24°C acclimated fish
467 (Supplementary Table S1, Supplementary Figure S2). This reduction in overall swimming performance

468 may have driven the high capture rate in the trawl at 24°C (Table 1, Figure 2, Supplementary Figure S1),
469 potentially masking any selection on individual swimming performance which may have been present
470 (Killen *et al.* 2013). While this is possible, decreases in overall fish activity were also recorded at 24°C
471 which is also likely to have increased overall capture probability, as fish become less likely to locate and
472 make use of available escape routes.

473 While population level increases in activity found at 20°could have driven high overall levels of
474 capture risk in the trap, individual level activity was not associated with trap capture vulnerability in any
475 instance (Table 2). This is surprising considering the potential links between traits related to activity and
476 the likelihood of a fish encountering and being caught by a fishing gear (Diaz Pauli *et al.* 2015).
477 Alternatively, selection on individual minnow's spontaneous activity may have been weakened by the
478 design of the fisheries simulations, which replicated the later stages of fisheries capture, after the fishing
479 gear had already been encountered by fish (Hollins *et al.* 2018). This may have decreased the capacity
480 for individual fish's activity to influence susceptibility to capture, as this trait may have been more
481 relevant in determining capture vulnerability during earlier stages in the capture process not examined
482 in the present study (by determining encounter rate with gears, for instance). If individual activity is an
483 important trait in determining capture vulnerability earlier in the capture process, then highest
484 encounter rates with gears in the wild may be expected at temperatures where spontaneous activity is
485 maximised, in this instance 20°C, before declining again as temperatures exceed thermal optima. Traits
486 related to space use and activity in fish can be under selection in passive fisheries (Monk and Arlinghaus
487 2017a), although this is not necessarily driven through a mechanism of more active fish encountering
488 fishing gears more frequently, as many fish encountering gears fail to be subsequently caught (Monk
489 and Arlinghaus 2017b). In this experiment, therefore, individual traits related to risk perception (e.g.
490 tendency for individual fish to approach a novel object) (Klefoth *et al.* 2017) may have been more
491 relevant in determining susceptibility. We found no relationship between any trait and risk of capture in

492 the trap, except at 24°C, where a negative relationship between swimming performance and capture
493 vulnerability was apparent (Table 4). This is despite traits related to foraging and exploration being
494 thought to be particularly relevant in determining vulnerability to capture by passive gears (Biro and
495 Post 2008; Hessenauer *et al.* 2015; Hollins *et al.* 2018; Klefoth *et al.* 2017; Koeck *et al.* 2018; Monk and
496 Arlinghaus 2017a; Monk and Arlinghaus 2017b). The negative relationship between swim performance
497 and capture vulnerability in the trap found at 24°C is difficult to explain, as no mechanism by which poor
498 swimming fish would be more likely to be caught by a trap is clear. It is possible that selection on
499 swimming performance by trapping is indirect, and instead related to a separate trait not measured in
500 this study but correlated with swim performance. It is possible that individual fish exhibiting the lowest
501 swim performance at 24°C were those experiencing the most severe effects of warm temperature
502 acclimation, and that these individuals were the furthest beyond their thermal optimum of the warm
503 acclimated fish. These particularly affected fish may have begun to exhibit behaviours which
504 subsequently increased their likelihood of capture, for example by increasing the perceived benefit of
505 food or shelter provided by the trap compared to less stressed fish.

506 While experimental approaches using simulated fisheries allow precise control over the factors
507 influencing fish capture vulnerability, the small scale at which they must be conducted means careful
508 consideration must be given to how the data can be interpreted and used to inform fisheries in the wild
509 and studies at larger scales. Recreating all stages of fisheries capture (Hollins *et al.* 2018) is generally
510 beyond the scope of experimental approaches. For example, individual traits determining habitat
511 selection are likely relevant during early stages of fisheries capture, as these will determine which fish
512 overlap with a deployed fishing gear (Olsen *et al.* 2012; Villegas-Ríos *et al.* 2018). Further issues of scale
513 arise regarding the size of the fishing gears relative to the fish themselves. While the size of the trap
514 relative to the minnows used in this experiment is comparable to that seen in trap fisheries in the wild
515 (Königson *et al.* 2015), the relative size of the trawl is much smaller than what would be expected in

real-world fishery. This likely exacerbated the impact of escape routes being present around the trawl in disrupting any potential selection on swimming performance. While fish can escape capture by manoeuvring outside of the path of a pursuing trawl, the fish which do are typically already close to the edges of the trawl mouth (Winger 2010). More typically, fish targeted by the trawl are herded into the centre of the pursuing net mouth by the trawl sweeps (Rose 1995; Ryer *et al.* 2009; Ryer 2008; Winger 2010), where the size of the trawl mouth relative to these pursued fish makes escape via manoeuvring outside of the path of the trawl more difficult.

To summarise, we found evidence that active and passive fishing gears exhibit distinct patterns of selection on fish behavioural traits, but no evidence of fisheries selection on physiological traits was found. Trawl simulations consistently selected on individual fish activity, while traps tended to be non-selective on individual traits until fishing trials were conducted at the highest acclimation temperature. Selection in both the trawl and trap fishery was altered at 24°C, driven by a combination of temperature effects on gear capture efficiency, and on underlying traits of the fish themselves. This study highlights the capacity for different fishing gears to select on distinct groups of phenotypic traits, but also shows that relationships between individual traits and vulnerability to capture may be modulated by environmental conditions.

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	Time		
Tank ID	T1 11.05.2017-02.06.2017	T2 06.07.2017-04.08.2017	T3 07.10.2017-28.10.2017
1 2 3	16°C Swim Performance Metabolic Phenotype Activity	16°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability	16°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability
4 5 6	16°C Swim Performance Metabolic Phenotype Activity	20°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability	24°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability

Figure 1: Timeline showing the acclimation of fish to different temperatures. In each case, fish were allowed to acclimate to each temperature for 4 weeks before measurements of individual traits began. At T1 fish were profiled for metabolic phenotype, swim performance, and behavioural traits, while each of these measurements was also repeated at T2 and T3. At T2 and T3, fish were additionally assayed for vulnerability to capture in both a trawl and trap simulated fishery. Note that during the final acclimation, a total of 9 fish died before respirometry or capture vulnerability assays could be performed at 24°C.

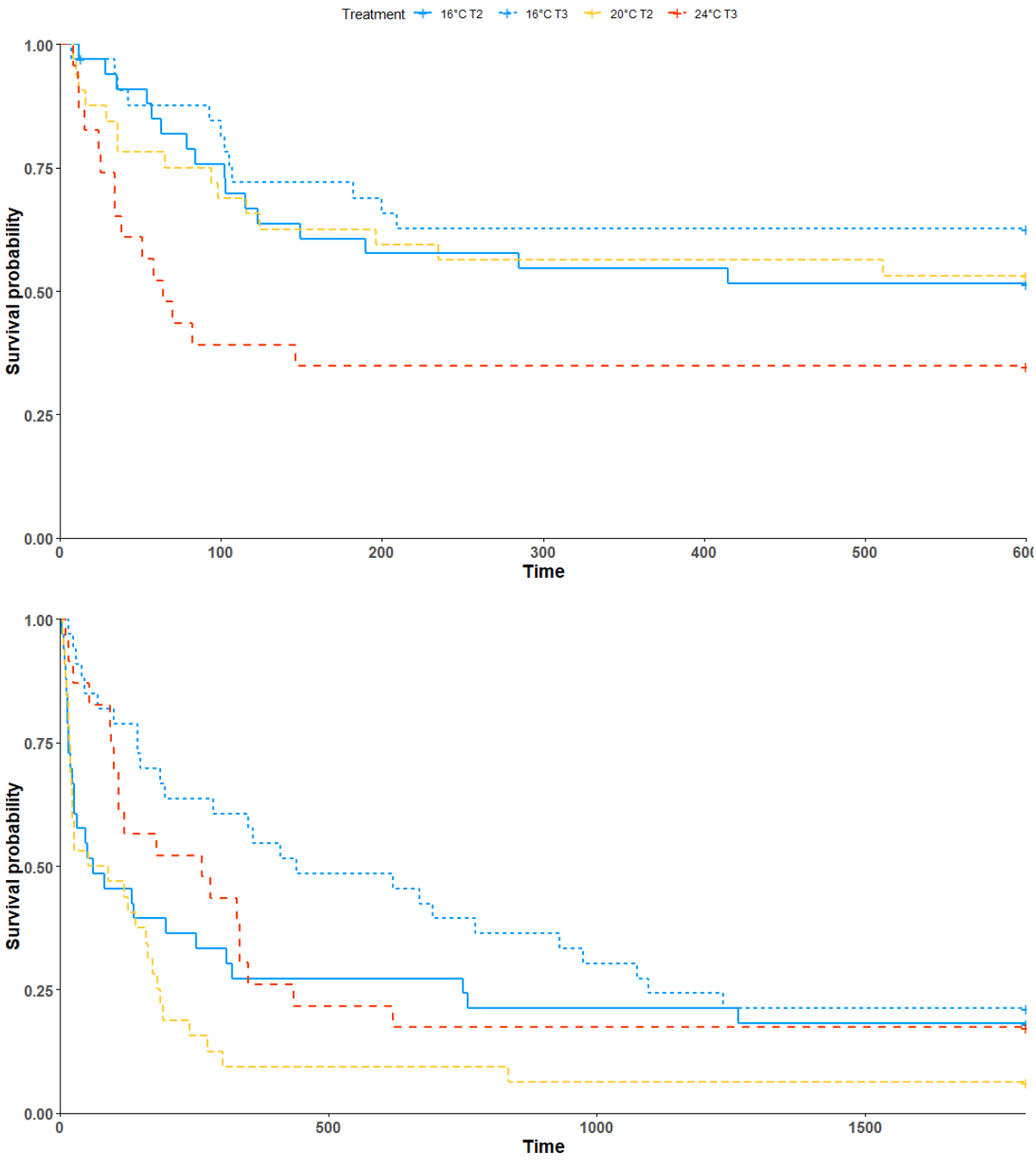

Figure 2: Kaplan Meier survival curves of minnow within simulated trawl (top) and trap (bottom) fisheries tested at different temperatures.

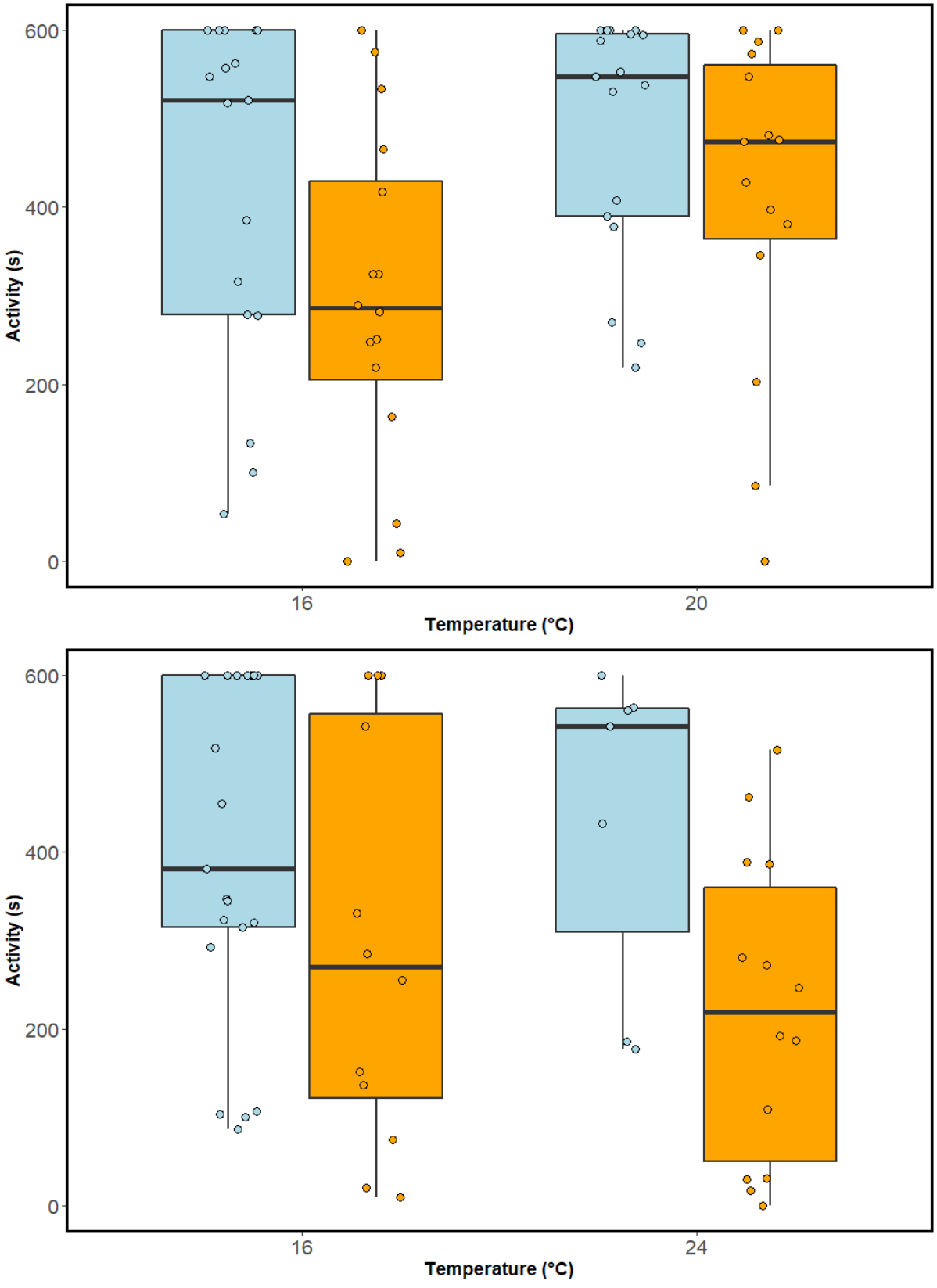

Figure 3:Boxplot of uncaught (blue) and caught (orange) fish activities in the trawl at 16 vs 20°C (top), and 16 vs 24°C (bottom)

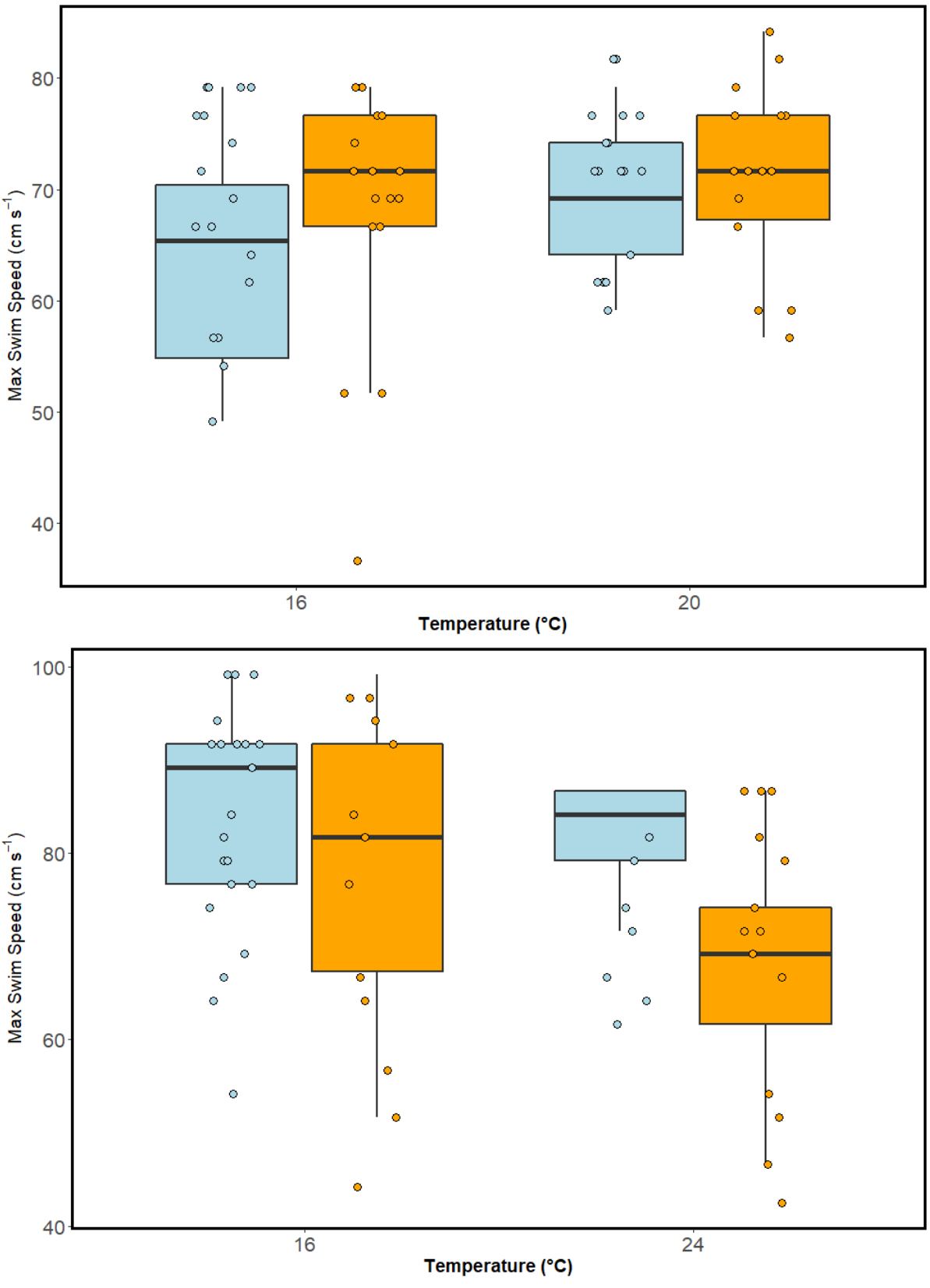

Figure 4:Comparison of of uncaught (blue) and caught (orange) fish swim speeds in the trap at 16 vs 20°C (top), and 16 vs 24°C (bottom)

Tables and Figures

Gear Type	Temperature Comparison	β	z	*p*
Trawl	16 vs 20	-0.07716	-0.215	0.83
	16 vs 24	0.985	2.524	0.0116
Trap	16 vs 20	0.3433	1.292	0.196
	16 vs 24	0.4073	1.335	0.182

Table 1: Results of Cox proportional hazards models examining the role of temperature in determining overall probability of capture in trap and trawl fishing gears. Comparisons are made within each gear type at each stage of the experiment.

Model	Term	β	z	*p*
Trawl 16T2	*adj(AS)*	4.51	1.829	0.067
	adj(MMR)	-4.36	-1.823	0.068
	SGR	-4.03	-1.244	0.213
	Log(Activity)	-0.371	-2.049	0.04
Trawl 16T3	*Log(Activity)*	-0.531	-2.278	0.025
Trap 16T2	*adj(SMR)*	-7.833	4.757	0.091
	adj(AS)	-4.199	2.643	0.117
	adj(MMR)	5.091	3.147	0.111
	SGR	3.327	1.886	0.084
Trap16T3	*SGR*	4.335	1.674	0.079
Trawl 20T2	*Log(Activity)*	-0.946	-2.34	0.005
Trap 20T2	*Null Model*	NA	NA	NA
Trawl 24T3	*Log(Activity)*	-0.358	-2.164	0.03
Trap 24T3	*Log (Umax)*	-0.04	-2.68	0.008

Table 2: Results of Cox proportional hazards models examining the role of individual behavioural traits in determining probability of capture in trap and trawl fishing gears.

Trait	*Adj. R*	*SE*	*CI*	*p*
Activity	0.462	0.078	0.296, 0.621	<0.001

Umax (BLs^{-1})	0.119	0.076	0, 0.272	0.069
Adj(SMR)	0	*NA*	*NA*	*NA*
Adj(AS)	0.298	0.082	0.145, 0.459	<0.001
Adj(MMR)	0.299	0.08	0.147, 0.456	<0.001

Table 3: Across context repeatabilities of individual behavioural and physiological traits assessed with LMEs using the trait of interest as a response variable, and acclimation temperature and fish ID as fixed and random effects, respectively.

Trait	***Agreement R***	***SE***	***CI***	***p***
Trawl Capture	0.19	0.148	0, 0.525	0.129
Trap Capture	0	1.76	0,7.117	0.5
Trawl Capture (16°C)	0.268	0.191	0, 0.639	0.122
Trap Capture (16°C)	0.017	0.336	0, 0.979	0.496

Table 4: Agreement repeatabilities of capture in each fishing gear. Binary caught/uncaught data for each gear type were used for the response variable in each case, using individual fish ID as a random effect.